

Larval Anatomy of Orussidae (Hymenoptera)

LARS VILHELMSSEN

Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100, Denmark,
e-mail: lbvilhelmsen@zmuc.ku.dk

Abstract.—The external and selected parts of the internal anatomy of the larva of *Orussus abietinus* (Orussidae) are examined. The external anatomy is similar to that reported for other Orussidae. The eyes, laterocervicalia, and thoracic legs are absent, and the antennae, maxillae, and labium are reduced. Each thoracic and abdominal segment has a pair of short transverse rows of recurved cuticular spines laterodorsally, probably for locomotory purposes. A previously unreported feature is the configuration of the hindgut, which has a set of transverse interlocking cuticular folds. The mid- and hindgut are anatomically continuous. Overall, the larval anatomy of Orussidae is highly reduced compared with that of other basal hymenopteran lineages and resembles that of apocritan larvae. The modifications of the larval anatomy are probably correlated with the shift in lifestyle from herbivorous to carnivorous, which is less demanding of the sensory, feeding, and locomotory apparatus.

Orussidae is a small wasp family, comprising 75 species worldwide (Vilhelmsen in press). Traditionally, the Hymenoptera have been subdivided in two suborders, the almost exclusively herbivorous ‘Symphyta’ and the predominantly entomophagous Apocrita; Orussidae were usually placed in the ‘Symphyta’ because of the absence of the wasp-waist in the adults, the defining feature of the Apocrita. However, recent phylogenetic treatments of the Hymenoptera unequivocally have retrieved Orussidae + Apocrita as an extremely well supported clade (Ronquist et al. 1999, Vilhelmsen 2001). Information on the biology of most species of Orussidae is scarce or non-existent; what evidence there is (see Vilhelmsen et al. 2001) indicates that the larvae are ectoparasitoids of woodboring insect larvae, usually Buprestidae (Coleoptera). This was probably the lifestyle of the common ancestor of all parasitoid Hymenoptera. The position of the woodboring ‘siricoid’ superfamilies as successive outgroups to the Orussidae-Apocrita clade indicates that the parasitoid lifestyle evolved via a woodboring in-

termediate in Hymenoptera (Hanson and Gauld 1995; Vilhelmsen 1997).

Nutall (1980) provided a very brief description of the larva of *Guiglia schauinslandi* (Ashmead, 1903), a New Zealand species. The only detailed descriptions of the immature stages of an orussid species are by Rohwer and Cushman (1917) and Parker (1935), who dealt with *Orussus occidentalis* Cresson, 1879, a Nearctic species. The section on Orussidae in Yuasa’s (1922) treatment of non-apocritan larvae is based entirely on Cushman and Rohwer (1917). They noted that the larva of *Orussus* share many traits with those of apocritan Hymenoptera (eyes, most head appendages, and thoracic legs very reduced), whereas the anatomy of adult Orussidae apparently resembles that of ‘Symphyta’. This mix of features and the parasitoid lifestyle led Rohwer and Cushman (1917) to erect a new suborder, the Idiogastra, comprising just the Orussidae.

Parker (1935) observed a few internal features of the head anatomy of *O. occidentalis*, but otherwise information about the internal larval anatomy of the family

is wanting. Orussidae were not included in the survey of 'symphytan' larvae by Maxwell (1955). Specifically, it is not known whether there is any connection between the mid- and hindgut. The separation of these gut sections and the postponement of voiding of the gut contents (as a meconium) until just prior to pupation is a near universal feature of the Apocrita (Hanson and Gauld 1995; Quicke 1997); it usually is interpreted as an important adaptation to the parasitoid lifestyle, especially endoparasitism, apparently serving to prevent contamination of the host. However, the condition in Orussidae and some of the putatively basal apocritan taxa (Stephanidae, Megalyridae) has not been investigated, making it impossible to deduce exactly when the feature arose in the evolutionary history of parasitic Hymenoptera.

In the present study, I investigate the larval anatomy of two species of Orussidae in some detail. In addition to the external features already described by Rohwer and Cushman (1917), selected internal features are examined. The findings are discussed in relation to features observed in other hymenopteran larvae.

MATERIALS AND METHODS

Larvae of *Orussus abietinus* (Scopoli, 1763) and *Guiglia schauinslandi* (Ashmead, 1903) were available for study. Unfortunately, only the material of the former was in good condition, having been collected recently (1998 or later) and preserved in 80% ethanol or Pampels fluid and subsequently transferred to ethanol. In total, five larvae of *O. abietinus* were examined. Of these, four were final instars or prepupae, collected in early spring prior to pupation, and one was an early instar collected later in spring on a moldy pupa of *Buprestis* sp. (Coleoptera, Buprestidae). Four larvae of *G. schauinslandi* were examined. All were in rather poor condition, having been preserved in 95% ethanol for 40+ years after having initially been col-

lected in a kerosene-acetic acid-dioxane solution (KAAD). Only a limited number of observations of the external anatomy could be carried out on these specimens.

External features.—Initial examination of external features on specimens kept in ethanol was carried out with a Leica MZ Apo dissection microscope.

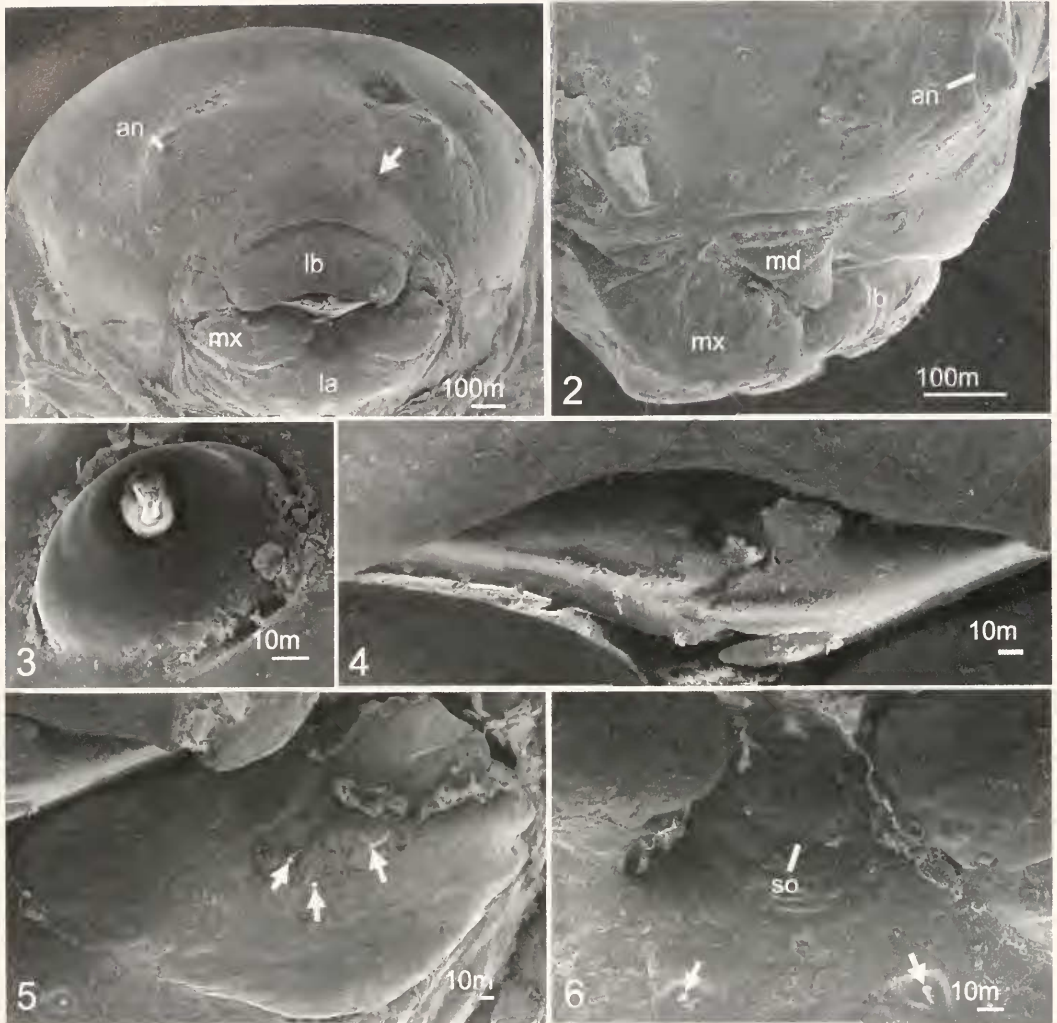
SEM.—Specimens preserved in ethanol were critically point dried and coated with Pt/Pd in a Jeol JFC-2300HR high resolution fine coater. They were examined with a Jeol JSM-6335F field emission scanning electron microscope.

Histological sections.—Specimens preserved in ethanol or Pampels fluid were dehydrated in butanol and embedded in paraplast. Sagittal sections of 8–12 μm thickness, depending on the size of the specimen, were cut with a microtome. The sections were treated in a trichrome stain (Weigert's haematoxylin-bluish erythrosin-fast green, preceded by phosphomolybdic acid); permanent preparations were made in entellan.

RESULTS

The descriptions are based entirely on the prepupae and early instar of *O. abietinus*. The observations that could be made on the *G. schauinslandi* specimens did not reveal any significant differences between the two species.

Overall.—Body elongate, dorsoventrally flattened (less conspicuous in early instar). Body outline in cross-section with distinct bend laterally between upper and lower surface. Head hypognathous, boundary between head and prothorax indistinct in early instar, especially laterally. Segment boundaries otherwise distinctly demarcated by deep furrows dorsally, especially on abdomen. Body cuticle wrinkled, but without regular transverse annuli or other regular intrasegmental subdivisions. Small trichoid sensilla scattered over body surface. All thoracic and abdominal segments dorsally with paired, transverse rows of 2–4 (early instar) or 3–5 (prepupa)



Figs. 1–6. *Orussus abietinus*, head anatomy. 1, 3–6. Prepupa. 1, Head, ventral view, arrow indicates position of anterior tentorial pit: an = antenna; la = labium; lb = labrum; mx = maxilla. 2, Early instar larva, mouthparts, lateral view: md = mandible (only base visible). 3, Antenna. 4, Tips of mandibles, ventral view. 5, Maxilla, arrows indicate trichoid sensilla (two leftmost broken). 6, Labium, arrows indicate trichoid sensilla: so = salivarial orifice.

slightly recurved cuticular spines submedially (Figs. 7–10).

Head.—Head capsule weakly sclerotized. Eye absent. Antenna one-segmented, short, rounded, situated lateroventrally on head capsule (Figs 1–2), distally with two short peglike sensilla in shallow depression (Fig. 3). Clypeus weakly delimited dorsally; anterior tentorial pits faintly visible as shallow, elongate depressions

(Fig. 1). Circular cuticular structure present medially of anterior tentorial pits, not visible externally. Small, transversely elongate sclerite present between clypeus and labrum. Labrum fleshy, slightly bifid apically, with 7–8 trichoid sensilla anterolaterally. Mandibular base broad, fleshy (Fig. 2), mandibular articulations displaced medially, not visible externally on head capsule. Distal part of mandible slen-

der and heavily sclerotized, arising medially from base, partly covered by labrum anteriorly and maxilla posteriorly (Fig. 2), terminating in three distinct cuticular teeth visible ventrally (Fig. 4). Maxilla undifferentiated, transversely elongate fleshy lobe, anteriorly abutting labrum; maxillary palp not developed, three trichoid setae situated in middle of maxillar lobe (Fig. 5). Labium narrow anteriorly, broadening posteriorly (Fig. 6), weakly delimited from maxilla by shallow oblique sulcus, retracted relative to maxillae. Salivarial orifice transverse slit surrounded by sclerotized cuticle (barely discernible in early instar larva), situated subapically on labium. Labial palp not developed, paired short trichoid sensilla present posterolaterally.

Thorax.—Laterocervicalia absent. Anterior thoracic spiracle well developed, apparently situated slightly anterior to boundary between pro- and mesothorax. Posterior thoracic spiracle vestigial, represented by small, elongate sclerotisation just posterior to meso/metathoracic boundary. Thoracic legs entirely absent.

Abdomen.—Ten segments present. Segments 1–8 with well developed spiracles situated laterodorsally (Fig. 7); spiracles circular, rim well sclerotized. Abdominal legs, suranal process, suranal hook, and subanal appendages absent. Anal slit situated posteriorly on segment 10, transversely elongate (Figs 9, 10), shallow (cannot be pried open with a fine needle).

Hindgut.—Posterior part of midgut of early instar larva with convoluted walls. Gut contents amorphous, with dark grains. Malpighian tubules not observed. Mid- and hindgut continuous (Fig. 11). Hindgut lined with unsclerotized cuticle becoming progressively thicker posteriorly. Anterior part of hindgut with somewhat thickened epidermis. Hindgut with walls straight, except for 10–12 narrow transverse cuticular folds posteriorly (Figs 11, 12); cuticular folds correspond to concavities in opposite wall. Most of hindgut

surrounded by muscular sheath, except for part posteriorly of cuticular folds (Fig. 12); sheath with transverse and outer longitudinal fibers. Prepupa similar to early instar except for following: Midgut with straight walls, apparently empty except for peritrophic membrane. Boundary between mid- and hindgut marked by one pair of malpighian tubules opening into lateral part of gut. Epidermis retracted from cuticle in posteriormost abdominal segment (Fig. 13), interspace between epidermis and cuticle occupied by amorphous material traversed by elongate tissue strands. Epidermis of anterior part of hindgut not thickened. Muscle sheath not extending very far along hindgut, not reaching region of cuticular folds, comparatively less developed than in early instar larva. Hindgut walls with 18–20 closely appressed cuticular folds (Fig. 14); folds transversely oriented medially, obliquely posteromedially oriented laterally.

DISCUSSION

The larva of *O. abietinus* closely resembles *O. occidentalis* (see Rohwer and Cushman 1917) in all external features; this is hardly surprising, since the two species are probably sister taxa (Vilhelmsen in press). The more distantly related *G. schauinslandi* does not differ significantly from *Orussus* spp. in the features that could be observed. However, all three species are comparatively derived within Orussidae, making inferences about the ground plan states for the family tenuous.

The larval head anatomy of Orussidae is highly reduced compared with other non-apocritan Hymenoptera. The eye is entirely absent (a condition also observed in 'siricoid' superfamilies), the antenna is one-segmented and of the mouthparts, only the mandibles appear to be functional, both the maxilla and labium having lost all traces of endites and palps and being immovable relative to the head capsule. In contrast, most 'Symphyta' have multi-segmented antenna as well as dif-

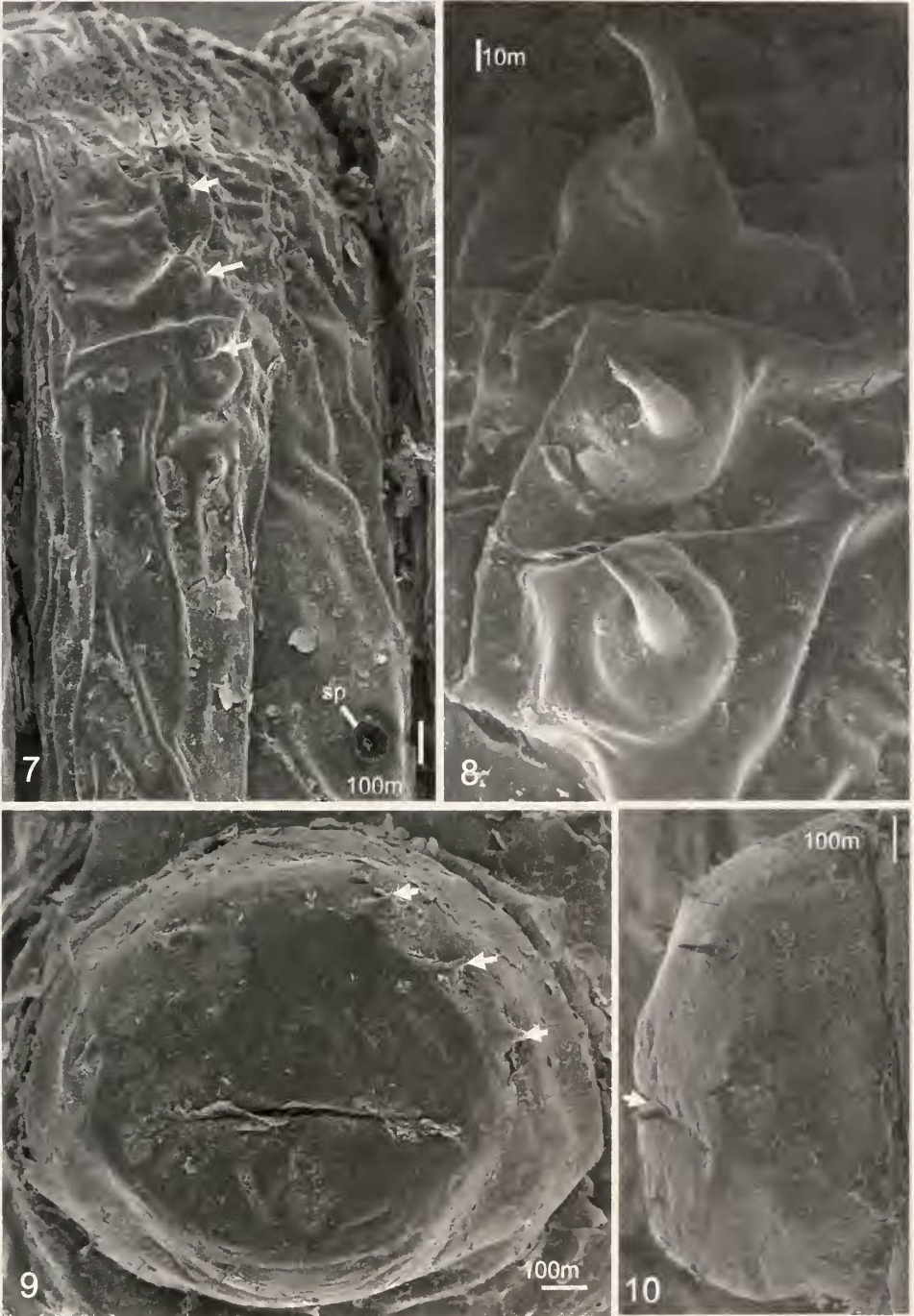
ferentiated endites and palps on the maxilla and labium (see Yuasa 1922). The mandibles of herbivorous 'Symphyta' are usually well sclerotized throughout with external articulations and broad shearing teeth distally. The condition of the mandibles (partly concealed by labrum and maxilla, proximal part unsclerotized, distal part narrowed, see also Rohwer and Cushman 1917, fig. 2a) observed in Orussidae is apparently similar to that of *Schlettererius cinctipes* (Cresson) (Stephanidae; Short 1978, fig. 20; Taylor 1967). Generally, the head anatomy of orussid larva is much closer to that of Apocrita than of other 'Symphyta'. With regard to maxillar and labial palps, those of Orussidae are even more reduced than some Apocrita (e.g., some Ichneumonoidea (Finlayson 1987) and Aculeata (Evans 1987; McGinley 1987)), which have papilliform, one-segmented palps.

The thoracic and abdominal anatomy of the larvae of Orussidae and Apocrita are also reduced relative to more basal Hymenoptera. The laterocervicalia, which in representatives of most 'symphytan' superfamilies articulates with the head capsule anteriorly and connects to the pronotum posteriorly (Vilhelmsen unpubl.), is entirely absent in Orussidae (see also Parker 1935) and apparently also in Apocrita, providing a closer integration of the head and thorax in the two latter taxa. The thoracic legs are entirely absent, having become progressively reduced within the basal lineages of the Hymenoptera (Vilhelmsen 2001). A suranal process, a heavily sclerotized projection on the 10th abdominal segment dorsally of the anal slit prominent in Cephidae, Anaxyelidae, Siricidae, and Xiphydriidae (see Yuasa 1922, pl. xii) is absent from Orussidae and Apocrita. The transverse rows of cuticular spines dorsally have been reported only from *Schlettererius cinctipes* (Stephanidae; Taylor 1967) outside the Orussidae, although in this species, they are only present in the prepupa. Their function in

orussid larvae is perhaps to facilitate movement along wood galleries, increased leverage being provided by the deep dorsal furrows between the body segments. Cooper (1953) observed oviposition by female *Orussus* in wood galleries some distance from potential hosts; he interpreted this as indicating that the larvae might be frass feeders. Alternatively, the early instar larva might actively seek out the host within its galleries, if the female was unable to reach the host with its ovipositor; this possibility was considered but rejected by Cooper.

Given the well corroborated monophyly of Orussidae + Apocrita, the interpretation of the phylogenetic significance of the shared reductional features in the larval anatomy is fairly straightforward: they represent synapomorphies for these two taxa. Some of these characters have already been included in recent phylogenetic treatments of the Hymenoptera (e.g., number of larval antennal segments, reduction of larval thoracic legs, characters 224 and 228 in Vilhelmsen 2001), whereas as others (reduced maxillar and labial appendages, absence of laterocervicalia) have been ignored until now.

The functional significance of the anatomical modifications can be interpreted in the context of the shift in larval lifestyle from herbivorous/woodboring to carnivorous/parasitoid having taken place in the common ancestor of Orussidae and Apocrita. The reduced sensory capabilities (loss of eyes, reduction of antennae) reflect the confined habitat (galleries in wood) of the larvae of the earliest parasitoid wasps and their closest relatives, the woodwasps. The reduction of the mouthparts is perhaps a consequence of the shift in food source from particulate plant matter that requires considerable handling and chewing to a much less demanding diet of insect body fluids. Once an ectoparasitoid wasp larva is in contact with its host, it is required to do little more than puncture the integument of the latter to gain access



Figs. 7-10. *Orussus abietinus*, abdominal anatomy. 7-8, Early instar larva, posterior to the left. 7, Dorsal part of abdominal segment: arrows indicate cuticular spines; sp = spiracle. 8, Recurved cuticular spines. 9-10, Prepupa. 9, 10th abdominal segment, posterior view, arrows indicate cuticular spines. 10, Same, lateral view, arrow indicates anal slit.



Figs. 11–14. 1 *Orussus abietinus*, internal anatomy of hindgut (posterior to left). 11–12. Early instar larva. 11, Overview of hindgut region, arrow indicates transition between mid- and hindgut; mus = muscle sheath. 12, Details of cuticular folds in hindgut. 13–14, Prepupa. 13, Overview of hindgut region, arrow indicates transition between mid- and hindgut, rectangle indicates approximate extent of Fig. 14; epi = retracted epidermis. 14, Details of cuticular folds in hindgut.

to its contents, a purpose for which the narrow, pointed mandibles of the orussid larva probably is admirably suited. The reduction of the locomotory apparatus again reflects the confined larval habitat, being taken even further than in the Cepidae and woodwasp families, which retain vestiges of thoracic legs. The suranal process present in these taxa is also absent in Orussidae and Apocrita, a change that perhaps is correlated with the shift in food source. This feature is needed as a brace by the endophytophagous taxa when chewing a tunnel through tough plant material; the larvae of Orussidae and wood-living Apocrita do not chew their own tunnels and hence do not need a posterior brace.

The configuration of the hindgut in the early instar larva and prepupa of *Orussus* is unlike anything else reported from Hymenoptera. The cuticular folds matching concavities in the opposite walls and the extension of the muscular sheath surrounding the hindgut to include the part with the folds indicate that even though the mid- and hindgut are not anatomically separated, the larva is able to close the hindgut by muscular action. In the prepupa, the opposite walls of the hindgut abut in the region with the cuticular folds even though the muscular sheath does not extend this far back; this may be caused by the loosening of the prepupal cuticle and the retraction of the epidermis and associated musculature prior to pupation.

The connection between mid- and hindgut in 'Symphyta' whose embryology have been examined (e.g., *Pontania caprae* Linnaeus (Tenthredinidae), see Ivanova-Kasas 1959) is established already at the time of hatching from the egg. The anatomical separation caused by the failure of the two gut sections to join during the embryological development (Hanson and Gauld 1995) has been reported from a wide range of apocritan superfamilies: Ceraphronoidea (Megaspilidae: *Dendrocerus* (= *Lygocerus*) spp., see Haviland 1920a, fig. 14), Chalcidoidea (Pteromalidae: *Spalangia muscidarum* Richardson, see Richardson 1922, fig. 7; *Asaphes vulgaris* Walker, *Pachycrepis clavata* Walker, see Haviland 1922), Cynipoidea (Figitidae: *Charips* spp., see Haviland 1920b, fig. 11a), Ichneumonoidea (Ichneumonidae: *Pimpla turionellae* (Linnaeus), see Führer and Willers 1986, fig. 3), Platygastroidea (Platygastridae spp., see Marchal 1906, pl. xviii: 24), Proctotrupoidea (Proctotrupidae: *Phaenoserphus viator* (Haliday), see Eastham 1929, fig. 12). It is often accompanied by considerable differentiation between hindgut regions (epidermis and muscle layer of variable thickness, formation of valves; e.g., Eastham 1929, Führer and Willers 1986, Haviland 1920b) that is less conspicuous in *O. abietinus*. However, many 'Symphyta' also have the hindgut differentiated into several regions (Maxwell 1955).

The functional and phylogenetic significance of the larval hindgut anatomy of *Orussus* is difficult to interpret without further information about the orussid lifestyle and investigation of larvae of some of the basalmost apocritan ectoparasitoid taxa (e.g., Stephanidae and Megalyridae). It is possible, but entirely conjectural, that the cuticular folds help the orussid larva to clamp its hindgut shut for most of its development, thus preventing contamination of its host. However, the expulsion of a meconium prior to pupation as seen in most apocritans examined was not observed in a couple of hatchings of *O. abie-*

tinus (Vilhelmsen unpubl.). The anatomical position (posteriorly in the hindgut) of the cuticular folds in *Orussus* is not homologous with the position (boundary between mid- and hindgut) of the separation of the gut sections in Apocrita, making it unlikely that the latter evolved from the former. Thus, this study has revealed another intriguing feature occurring in parasitic Hymenoptera, rather than elucidating the evolution of an already known trait.

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